HILGARDIA

A Journal of Agricultural Science Published by the California Agricultural Experiment Station

VOL. 19 MARCH, 1949 No. 2

THE BIOLOGY OF THE STRAWBERRY ROOTWORM IN CALIFORNIA[1]

LESLIE M. SMITH[2] AND GEORGE S. KIDO[3]

INTRODUCTION

THE STRAWBERRY ROOTWORM, *Paria canella quadrinotata* (Say), is a serious pest of strawberries and raspberries in California. Its biology was studied intensively in the Santa Clara Valley from 1939 through 1942, when World War II, and the consequent reduction in berry acreage, caused work on the problem to stop. The results of the study of the strawberry rootworm are now reported in this paper.

Since the war there has been a marked increase in berry acreage, with an accompanying increase in actual and potential damage by the strawberry rootworm. Further studies were therefore conducted on control during the past three years, and these will be reported in another paper.

GEOGRAPHICAL DISTRIBUTION

The strawberry rootworm is probably indigenous to North America, since it has been reported only from the United States and Canada. Published reports indicate its presence in Alabama, Arizona, California, Connecticut, District of Columbia, Illinois, Indiana, Kansas, Louisiana, Maine, Maryland, Massachusetts, Michigan, Mississippi, Missouri, Montana, Nebraska, New Jersey, New Mexico, New York, North Carolina, Ohio, Pennsylvania, Rhode Island, Tennessee, Texas, Virginia, and Wisconsin. From its known distribution, the pest may be assumed to occur throughout the entire United States. Its distribution in the United States is shown in figure 1.

In California, the strawberry rootworm occurs in Alameda, Contra Costa, Merced, Monterey, Placer, Sacramento, San Benito, San Francisco, San Joaquin, San Mateo, Santa Clara, and Yuba counties.

[1] Received for publication May 21, 1948.

[2] Associate Professor of Entomology and Associate Entomologist in the Experiment Station.

[3] Entomologist, Wisconsin Alumni Research Foundation.

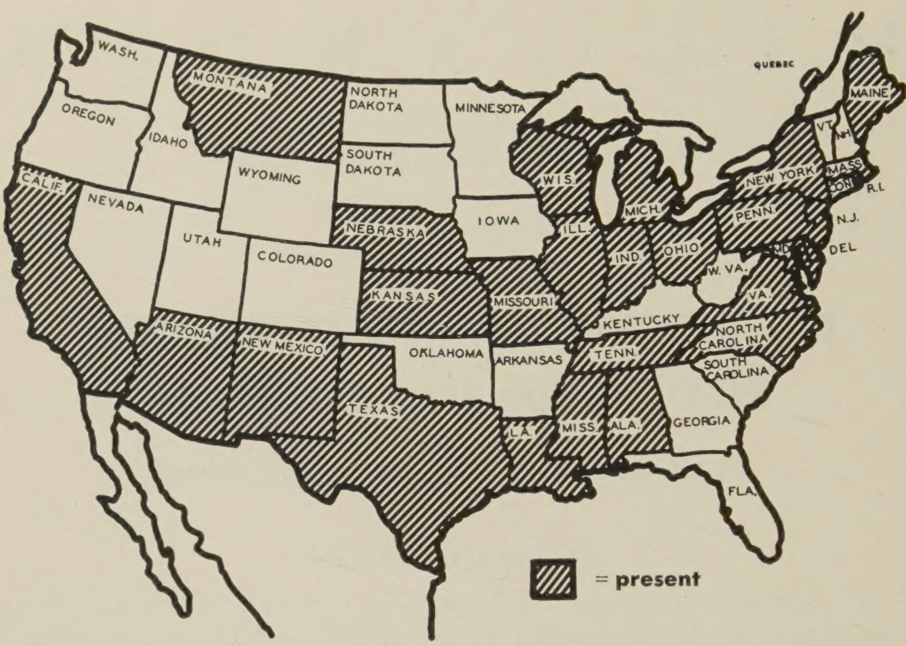

Fig. 1.—Known distribution of the strawberry rootworm in the United States.

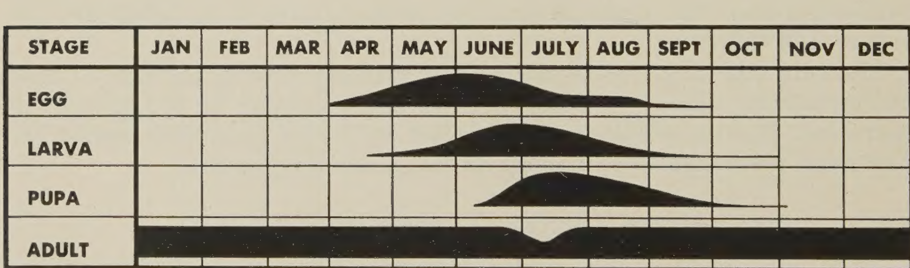

Fig. 2.—Occurrence of the several stadia of the strawberry rootworm throughout a year.

SEASONAL CYCLE

The adult strawberry rootworm is a beetle; all these beetles are females. They overwinter in dormant condition in the soil, and emerge in the spring when they feed voraciously on the foliage of both strawberries and raspberries. Their eggs, laid in groups, soon hatch into white, six-legged larvae which penetrate the soil and feed on the roots of the plants. By midsummer the larvae reach full growth, pupate, and emerge as new adults. These adults feed on the foliage during the late summer and fall, then hibernate during the winter. New adults do not lay eggs prior to hibernation. The yearly cycle of the strawberry rootworm is shown in figure 2.

The several aspects of this cycle which have been studied in detail are reported in this paper.

HOST PLANTS

A wide variety of plants is recorded as hosts of the strawberry rootworm in the United States. Weigel (1926) lists peach, heath aster, oats, millet, strawberry, butternut, black walnut, Japanese walnut, juniper, wild crab apple, apple, cinquefoil, rose, raspberry, blackberry, rye, mountain ash, and grape. Readio (1939) reported it on English walnut.

In California the strawberry rootworm feeds only on strawberries and brambles. In one isolated instance, it was known to feed, to a limited extent, on a single grapevine growing in a heavily infested raspberry patch. In several instances, after the beetles had completely defoliated a raspberry patch, they were observed feeding to some extent on the foliage of wild morning glory growing in the patch.

All varieties of strawberries observed in this investigation were attacked by the beetle, with no varietal preference indicated. Among brambles, the St. Regis red raspberry was most frequently found to be damaged, but this variety was the one generally grown in the area studied. Severe infestations were seen on black raspberry, Boysenberry, Himalaya blackberry, and Youngberry. Cuthbert and LaFrance red raspberries, on the other hand, were only slightly damaged when growing next to severely damaged St. Regis red raspberries.

In the eastern part of the United States, the strawberry rootworm is a serious pest of greenhouse roses. In California it has never been found feeding on roses, although when adult beetles were confined in a battery jar with only rose leaves for food, they fed extensively on the leaves.

ADULT STADIUM

Hibernation. The adult beetles (fig. 3) pass the winter on or in the ground. In raspberry patches most of them are found in surface rubble, particularly in the tightly curled edges of dried leaves, in hollowed canes, or in any interstice large enough to admit their bodies. Some are found under the highest and driest clods on the crown of a hedgerow; wormholes in such clods are especially favored for hibernation.

An attempt was made in this study to delimit the period of hibernation. During the fall, winter, and spring, a group of 50 beetles was caged in a gallon-sized battery jar where corrugated paper had been placed in the bottom to provide hiding places. In the jar were suspended a humidifying vial and a bouquet of fresh strawberry leaves in water. The jar was then covered with thin cloth and placed in an open-front wooden box in a lath house where it had no direct sunlight. At intervals the leaves—which hung near the top of the jar—were removed, the feeding holes counted, and fresh leaves placed in the jar.

All beetles in this test survived the winter except one, which died on February 2. The results of the test are given in table 1. These data indicate that the beetles may become active and feed in midwinter during warm periods. In this test, appreciable feeding ended on December 3 and was not resumed until February 23. This represents a nonfeeding hibernation period of 82 days.

In strawberry patches the beetles usually hibernate in the crown of the plants, often wedging themselves in between the leaf bases, and usually below the top of the soil.

Beginning of Spring Activity. Although the beetles may remain motionless during the winter months, they can be restored to full summer activity within a few minutes in an artificially warmed environment. This can occur at any time during hibernation. Even on warm days in winter, some activity was seen in the field. For instance, feeding was observed in the field as late as November 16 and as early as January 30.

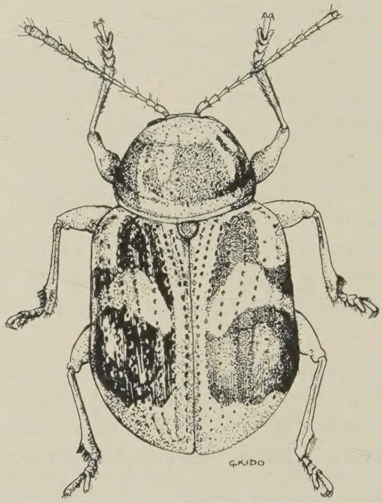

Fig. 3.—Adult of the strawberry rootworm. (Twelve times natural size.)

The period of time elapsing between emergence from hibernation and the beginning of oviposition is of prime importance when considering methods of preventing strawberry rootworm damage. The rate of defecation was decided upon as a possible index to the amount of prior feeding. A study was therefore conducted of frass and rates of frass production.

The individual coprolites are irregularly cylindrical, their length averaging approximately three times their diameter. While they vary somewhat in size, a random sample of 20 coprolites approaches the common average very closely. The ashing of air-dry frass and fresh strawberry leaves disclosed that 33.602 grams of leaves yielded 1 gram of ash; and 8.938 grams of frass yielded 1 gram of ash. Therefore, 1 gram of frass represents 3.760 grams of leaves; and 1 gram of leaves represents 0.232 gram of frass. Since adult beetles do not increase in weight, they probably do not retain ash constituents for body building. A small amount of ash probably goes into the development of the eggs, but this is believed to be a very small fraction of the total ash consumed. Therefore, the above conversion of frass and leaves is believed to be nearly correct. Since a total of 5,558 pellets of frass weighed 56.8 milligrams, an average pellet would weigh 0.01023 milligram.

To study spring emergence from hibernation by measuring frass production it was necessary to study the production of frass from a single meal.

Fifty hibernating beetles were collected in the field on February 9 and isolated, 1 in each of 50 vials. They were held at room temperature, which restored them to normal spring activity. For 24 hours, beginning February 12, they were fed fresh strawberry leaves, then were not fed again during this test. The measurements of frass produced are summarized in table 2.

TABLE 1

HIBERNATION PERIOD OF 50 STRAWBERRY ROOTWORM BEETLES MEASURED BY AMOUNT OF FEEDING

Date	Number of holes	Holes per day	Date	Number of holes	Holes per day
November 1	181	60.3	December 24	0	0.0
November 5	290	72.5	December 31	0	0.0
November 10	210	42.0	January 8	2	0.3
November 12	17	8.5	January 16	0	0.0
November 19	64	9.1	January 26	0	0.0
November 26	29	4.1	February 2	0	0.0
December 3	39	5.6	February 15	7	0.5
December 10	1	0.1	February 23	8	1.0
December 17	0	0.0	March 16	150	6.8
December 22	0	0.0	March 23	329	41.1

TABLE 2

FRASS PRODUCTION BY 50 STRAWBERRY ROOTWORM BEETLES FED ON FEBRUARY 12 ONLY

Date of frass production	Pellets		Beetles defecating	
	Number	Average	Number	Per cent
February 10	14	0.28	2	4.0
11	2	0.04	2	4.0
12	3	0.06	2	4.0
13	585	11.7	50	100.0
16	610	12.2	50	100.0
17	15	0.3	13	26.0
18	7	0.14	7	14.0
19	2	0.04	1	2.0
Total	1,238	24.76	127	

From these data it can be concluded that 2 of the 50 beetles had fed before capture in the field. Water without food did not stimulate frass production. A meal most frequently led to the production of 24 pieces of frass, which would weigh 0.245 milligram, and would represent the consumption of 0.923 milligram of leaf tissue.

After the above facts were established, it was possible to collect a sample of beetles in the field, isolate each in a vial, and, by measurement of frass produced, determine whether or not the specimen had fed. Fifty beetles were collected and isolated at approximately weekly intervals from February 9 to March 25. The numbers which fed prior to capture are given in table 3. There is a fluctuation in the average number of pellets per active beetle shown in

the first three collections. This may be caused by small numbers in the sample, or more probably by interfering weather conditions, such as rain or cold, which may have prevented the beetles from feeding just prior to February 18.

The data in table 3 are shown graphically in figure 4. By extrapolation, the earliest emergence from hibernation was probably February 7, and the process was practically complete by March 11. Any beetles hibernating at a considerable depth in the soil or in some other cool location might emerge much later. For practical purposes the emergence period may be considered to be approximately 33 days.

Strawberries support some green leaf tissue throughout the winter. Raspberries begin to leaf out in the first half of February. Usually new raspberry suckers emerge from the soil prior to the opening of the cane buds. Consequently, food is available to the adult beetles at the time they emerge from hibernation.

TABLE 3

BEGINNING OF SPRING ACTIVITY OF 50 STRAWBERRY ROOTWORM BEETLES

Date collected	Number previously fed	Per cent active	Average pellets per active beetle
February 9	2	4.0	6.50
February 18	22	44.0	2.45
February 25	28	56.0	3.64
March 3	41	82.0	4.39
March 11	48	96.0	3.94
March 17	47	94.0	4.66
March 25	47	94.0	4.40

Preovipositional Period. Although the correct use of the term "preovipositional period" indicates the time which elapses from the beginning of the adult stadium until egg laying, it is used here to indicate the period between emergence from hibernation and egg laying. This is the most important period for control of the pest.

Thirty beetles were removed from hibernation out of doors, and were isolated, 1 in each of 30 vials in the laboratory on February 4. They were fed fresh strawberry leaves and water daily, and the amounts of frass and eggs produced were measured. Table 4 shows the time which elapsed between the beginning of spring activity and the first eggs produced (based on 8 typical specimens). This period ranged from 29 to 43 days and averaged 32.3 days. The time elapsing between the production of the second, third, and fourth batches of eggs is included in table 4 for comparison with the preovipositional period. The averages ranged from 2.9 to 5.9 days and averaged 4.5 days in contrast to the preovipositional period of 32.3 days. During the preovipositional period, the 8 beetles consumed 12.71 milligrams of leaf tissue (computed from frass production) or an average of 1.74 milligrams of food per egg laid in the first batch. The next three batches of eggs were laid after eating 0.33 milligram of food per egg.

Egg Production. The beetles lay their eggs between two adjacent surfaces, which are separated by about the width of the base of the ovipositor. They insert several eggs into the carefully selected crevice, then secrete a shallow crescentic wall of black substance which partially encircles the egg mass. This material soon hardens and doubtless serves as a protection against predators.

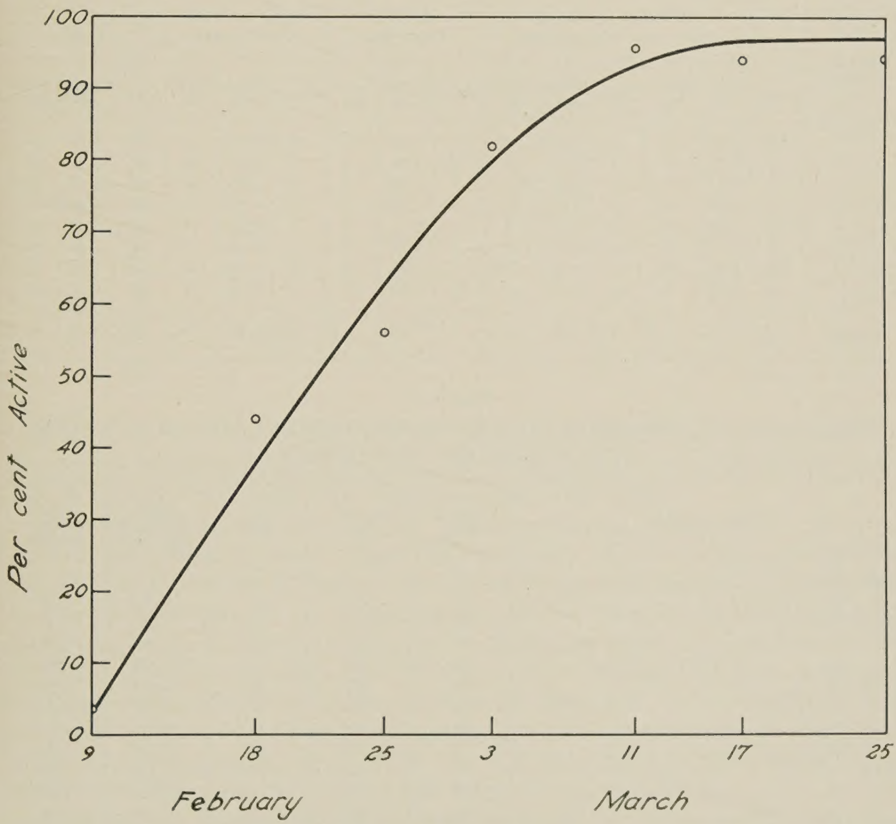

Fig. 4.—Beginning of spring activity of the strawberry rootworm based on measurement of frass.

To provide egg niches of suitable width, the beetles were supplied with paired glass microscope slides touching at one end and separated by the width of a number 2 insect pin at the other end. The distance between the slides therefore graduated uniformly from zero at one end to the width of the pin at the other. The beetles selected a place at which the width between the slides was suitable and inserted their eggs. Then the investigator could examine the slides with a microscope and easily count the eggs.

To determine the time of day when eggs were laid, a group of 50 beetles was placed in a 1-gallon battery jar with glass slides prepared as described. The jar was kept under natural conditions, then observed on June 12. No eggs were laid during the day. The first eggs were laid at 6 :30 p.m. Egg production

reached a maximum at 7:15 p.m., then decreased, and ceased at 11:00 p.m. Between 11:00 p.m. and 6:00 a.m., only one egg mass was deposited.

Number of Eggs Produced. To determine the number of eggs laid under conditions of outdoor temperature, 100 beetles were placed in a 1-gallon battery jar in a standard weather-bureau kiosk on February 13. They were fed, watered, and examined for eggs at approximately weekly intervals. A few eggs were found on March 28, but no others were laid until April 19. By August 9 only 16 beetles remained alive, and these laid no more eggs. The record of their egg production is given in table 5. One average beetle laying the average number of eggs throughout the time shown in this table would have laid 33.62 eggs. This figure, which is considerably lower than the figures obtained under other conditions, may be due to infrequent feeding.

TABLE 4

PREOVIPOSITIONAL PERIOD OF 30 STRAWBERRY ROOTWORM BEETLES

Beetle number	First eggs			Second eggs			Third eggs			Fourth eggs			Total		
	Days	Frass, mg	Number	Days	Frass, mg	Number	Days	Frass, mg	Number	Days	Frass, mg	Number	Days	Frass, mg	Number
1	30	2.85	2	3	0.05	7	8	1.72	15	2	0.76	5	43	5.38	29
2	35	4.13	7	6	0.87	12	2	0.28	7	4	0.21	12	47	5.49	38
3	29	3.27	8	4	0.47	10	4	1.32	2	7	1.16	10	44	6.22	30
4	30	2.94	9	3	0.37	12	8	1.75	3	2	0.49	3	43	5.54	27
5	33	3.00	14	8	1.67	4	1	0.15	7	1	0.31	7	43	5.13	32
6	29	2.57	5	4	0.28	12	7	0.96	12	3	0.78	7.	43	4.59	36
7	43	5.19	8	4	0.70	12	3	0.88	8	1	0.33	0	51	7.10	28
8	29	3.05	5	6	0.69	12	14	1.86	17	3	0.68	13	52	6.27	47
Average	32.3	3.38	7.3	4.8	0.64	10.1	5.9	1.12	9.9	2.9	0.59	7.1	45.8	5.72	33.4

TABLE 5

EGGS LAID BY STRAWBERRY ROOTWORM BEETLES UNDER OUTDOOR TEMPERATURE CONDITIONS

Date observed	Beetles alive	Beetle-days*	Eggs laid	Eggs per beetle per day	One average beetle†
April 12	96	...	0	0	0
19	96	672	31	0.046	0.28
May 16	82	2,214	217	0.098	2.68
22	82	492	146	0.297	1.78
29	82	574	80	0.139	0.97
June 5	82	574	331	0.577	4.04
11	82	492	171	0.348	2.09
18	82	574	250	0.436	3.05
25	82	574	277	0.483	3.38
July 2	73	511	396	0.775	5.43
9	60	420	73	0.174	1.22
18	48	432	55	0.127	1.14
24	48	288	45	0.156	0.94
31	30	210	146	0.695	4.87
August 9	16	144	28	0.194	1.75
14	10	50	0	0.0	0.0

* Number of beetles × number of days between observations.

† Average eggs per beetle per day × number of days elapsed in that period. Total of this column is 33.62 eggs.

To determine the number of eggs produced per beetle under more satisfactory conditions, 30 beetles were placed, 1 in each of 30 cages, on February 4, and fed strawberry leaves and water throughout the rest of their lives. No eggs were laid until March 5, at which time only 18 beetles were still alive. The average number of eggs laid by these beetles is given in the following list:

For a 10-day period ending	Eggs per beetle per day
March 15	0.94
25	1.45
April 4	2.21
14	2.04
24	1.90
May 4	0.20
14	1.14
24	0.78
June 3	0.71
13	0.83
23	0.52

All of the beetles died by the first of July. One beetle laying eggs throughout the period between March 5 and June 29 at the rate shown as the 10-day average of eggs per beetle per day would have laid 126.2 eggs.

The detailed records for 7 of the beetles grouped in this list are given in table 6. This table shows that the number of eggs laid at one time varies from 1 to 18. The frequency of layings containing from 1 to 5 eggs was 21, frequency of from 6 to 10 eggs, 28; 11 to 15 eggs, 34; and 16 to 18, 13. In considering the time which elapsed between layings, it should be noted that no records are included in table 6 for days on which none of the beetles laid eggs. Although beetles occasionally laid on two consecutive days and, in one instance, laid only after a period of 18 days, the normal period between layings was 2 to 3 days. The average total eggs laid by the 7 beetles listed in table 6 was 137.3, which compares with the average 126.2 eggs based on table 5.

Eggs Laid at Various Constant Temperatures. To determine the influence of temperature on oviposition, beetles were held throughout the egg-laying period at constant temperatures of 60°, 80°, and 90° F. The relative humidity was held at 73 per cent. Three hundred beetles were placed in each gallon-sized battery jar, and one such jar was kept at each of the above temperatures. Throughout this test the beetles were fed strawberry leaves, arranged as bouquets, with petioles in water, packed with cotton. This provided a source of drinking water. The results are given in table 7.

These data show that egg deposition at 60° F began 70 days later than at 80° and 90°. The beetles at 80° laid few eggs between the one hundredth and the one hundred and fortieth days of the test. The reason for this is not known. Had this not occurred, the cumulated eggs per beetle for the entire period might have approximated 400, which would be more consistent with the 580 eggs laid at 90° F.

TABLE 6

RECORD OF EGGS LAID BY INDIVIDUAL STRAWBERRY ROOTWORM BEETLES

Date	Beetle number						
	1	2	3	4	5	6	7
March 5	4	..	..	5	..	5	..
6	..	9	..	..	..	..	..
9	..	12	14	..	..	..	..
12	..	..	..	12	..	..	..
13	..	..	..	..	..	12	..
17	..	3	4	12	..	..	..
18	..	..	7	..	..	..	11
19	..	3	7	..	18	..	..
20	..	5	..	7	..	..	..
23	7	10	14	..	..	..	6
25	..	..	6	..	..	17	..
26	..	..	..	14	18	..	..
27	..	8	..	..	..	..	..
28	16	..	12	..	..	13	..
31	..	8	..	..	16	16	..
April 1	..	17	..	..	..	..	..
2	3	..	..	..	..	..	..
3	..	..	..	14	..	..	11
6	..	10	9	..	..	..	..
7	2	10	11	9	4	2	..
8	..	..	..	..	..	..	16
9	..	..	..	9	15	..	..
10	..	5	16	8	..	..	..
13	17	14	..	..	13	..	15
14	..	..	11	..	..	..	..
15	..	14	..	17	..	..	..
16	..	..	..	..	6	..	..
17	..	..	10	..	..	..	..
18	..	9	..	..	..	..	..
21	6	10	13	2	15	..	..
22	..	..	..	18	..	..	15
23	..	11	..	..	..	..	..
May 1	..	..	..	3	..	..	..
4	..	8	..	..	..	..	..
5	..	10	10	..	..	..	9
8	..	10	..	..	..	..	13
12	14	..	..	..	..	..	..
13	..	10	..	13	..	..	..
15	..	..	D	..	..	D	3
20	..	8	..	5	..	..	15
25	..	..	..	11	..	..	15
26	17	2	..	..	D	..	..
29	..	1	..	..	..	..	..
June 1	2	..	..	..	..	..	..
4	..	..	..	..	..	..	15
9	3	..	..	4	..	..	..
10	..	..	..	..	..	..	15
15	..	..	..	..	..	..	14
18	..	D	..	..	..	..	..
23	..	..	..	D	..	..	..
29	D*	..	..	..	..	..	13
30	..	..	..	..	..	..	D
Totals	91	207	144	163	105	65	186

* D = dead.

A group of 300 beetles was similarly held at 45° F and 73 per cent humidity. These beetles did not feed and did not produce a single egg. At 141 days from the start of this test, the last surviving adult in this temperature died.

The length of the ovipositional period was determined for 10 beetles caged separately at room temperature. The length of this period varied from 55 to 137 days with a mean of 91.0 days, as shown in table 8.

TABLE 7

EGGS PER BEETLE PRODUCED AT VARIOUS CONSTANT TEMPERATURES

Days elapsed	60° F		80° F		90° F	
	Eggs per period	Cumulative	Eggs per period	Cumulative	Eggs per period	Cumulative
0	0.0	0.0	0.0	0.0	0.0	0.0
10	0.0	0.0	0.12	0.12	0.49	0.49
20	0.0	0.0	1.90	2.02	10.51	11.00
30	0.0	0.0	7.09	9.11	31.96	42.96
40	0.0	0.0	30.24	39.35	42.79	85.75
50	0.0	0.0	37.57	76.92	39.97	125.72
60	0.0	0.0	39.22	116.14	47.29	173.01
70	0.0	0.0	28.37	144.51	32.49	205.50
80	0.09	0.09	12.03	156.54	44.21	249.71
90	0.03	0.12	2.12	158.66	49.30	299.01
100	0.22	0.34	1.01	159.67	45.89	344.90
110	0.17	0.51	0.46	160.13	26.03	370.93
120	0.85	1.36	0.33	160.46	24.83	395.76
130	1.28	2.64	0.17	160.63	13.06	408.82
140	3.63	6.27	0.85	161.48	14.63	423.25
150	12.74	19.01	1.41	162.89	21.50	444.95
160	15.47	34.48	3.04	165.93	32.66	477.61
170	16.86	51.34	4.95	170.88	56.62	534.23
180	19.04	70.38	9.77	180.65	38.50	572.73
190	29.62	100.00	9.11	189.76	7.68	580.41
200	31.55	131.55	6.06	195.82	0.0	580.41
210	26.45	158.00	2.50	198.32	0.0	0.0
220	21.62	179.62	2.56	200.88	0.0	0.0
230	12.47	192.09	2.00	202.88	0.0	0.0
240	5.85	197.94	3.26	206.14	0.0	0.0
250	2.84	200.78	2.30	208.44	0.0	0.0
260	0.08	200.86	1.30	209.47	0.0	0.0
270	0.08	200.94	1.52	211.26	0.0	0.0
280	0.05	200.99	1.06	212.32	0.0	0.0
290	0.0	200.99	1.87	214.19	0.0	0.0
300	0.0	200.99	0.0	214.19	0.0	0.0

TABLE 8

LENGTH OF OVIPOSITIONAL PERIOD

	Total eggs per beetle	Eggs per batch		Ovi-positional period, days
		Maximum	Minimum	
Minimum	29	10	1	55
Maximum	207	20	6	137
Mean	109.1	15.5	3.3	91.0

The length of the postovipositional period was determined by holding 24 beetles in isolation cages at room temperature from the time they ceased egg laying until they died. The postovipositional period for these beetles ranged from 5 to 68 days, with a mean of 29.82 days (± 2.65).

Longevity. To determine the length of adult life, 32 beetles were collected in the field from pupal cells in the soil. Only teneral specimens were taken,

and, hence, none was over 2 days old. These beetles were kept in a gallon-sized battery jar in a standard weather-bureau kiosk, and, consequently, subjected to out-of-door temperatures. They were given strawberry leaves and water. Corrugated paper was placed in the jar to furnish hibernation quarters and daytime hiding places. This test was started on July 16, 1941, and terminated on December 3, 1942. Fifteen of the beetles died by the end of September, 1942, and 17 lived through the summer and entered hibernation for the second winter in 1942. Fourteen beetles were still alive on December 3, 1942, and the test was terminated. These adults had lived 506 days.

EGG STADIUM

The eggs are laid in groups or batches ranging from 1 to 20 eggs each. Table 8 shows that the largest batches laid by 10 beetles throughout their entire egg-laying period averaged 15.5 eggs each, and that the smallest batches averaged 3.3 eggs each.

Incubation Period. To determine the length of the egg stadium at room temperature, eggs were observed between paired glass slides as described above. Throughout the months of April and May, 50 batches of eggs were selected, one from each of 50 beetles. The time required for these eggs to hatch when held at room temperature is shown in the following list:

Incubation period (days)	Number of eggs hatched
9	0
10	4
11	9
12	13
13	6
14	5
15	55
16	26
17	23
18	31
19	10
20	9
21	2
22	0
23	5
24	0

These data show a minimum incubation period of 10 days and a maximum of 23 days. The weighted average is 16.97 days. Of the 340 eggs observed in this test, only 198 or 58.2 per cent hatched.

Incubation Period at Various Controlled Temperatures. Eggs laid by beetles in a constant temperature of 90°F were transferred immediately after being deposited to constant temperatures of 60°, 70°, 80°, and 85°F, where the humidity was 73 per cent. The length of the incubation period at these temperatures is shown in table 9 and figure 5.

TABLE 9

INCUBATION PERIOD OF EGGS AT VARIOUS CONSTANT TEMPERATURES

Temperature, degrees F	Eggs hatched, per cent	Hours elapsed	Days
60	50	520	21.7
	75	548	22.8
Room	50	377	15.7
	75	418	17.4
70	50	287	12.0
	75	319	13.3
80	50	172	7.2
	75	183	7.6
85	50	150	6.3
	75	160	6.7

The mortality, or per cent of eggs failing to hatch at these temperatures was 20.4 per cent for 60°F; 25.5 per cent for 80°; and 32.8 per cent for 85°. No egg hatched in a group incubated at 90°.

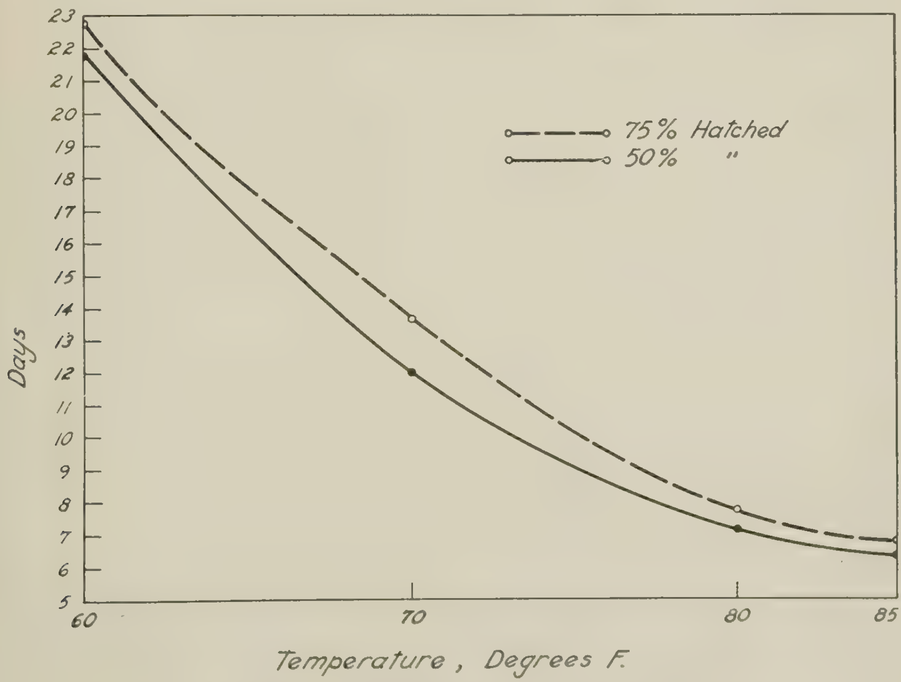

Fig. 5.—Incubation periods of the eggs of the strawberry rootworm at various constant temperatures.

LARVAL STADIUM

Location of Larvae in the Soil. Nine areas in an infested commercial raspberry patch were studied on May 23 to determine the depth at which the larvae (fig. 6) occur in the soil. Six areas in a commercial strawberry patch were similarly studied on June 14. The soil was removed in horizontal layers, each 1 inch thick, and carefully examined for larvae. The results are given in table 10. No larvae were found below 8 inches in either case. Horizontally, the larvae are found only within the ramifications of the roots of the host, and are more abundant at the center than at the periphery.

TABLE 10

LOCATION OF LARVAE IN THE SOIL

Depth in inches	Raspberry		Strawberry	
	Number	Per cent	Number	Per cent
1	3	4.0	33	34.0
2	28	37.3	22	22.7
3	29	38.7	21	21.6
4	13	17.3	15	15.5
5	2	2.7	2	2.1
6	0	0.0	1	1.0
7	0	0.0	3	3.0
8	0	0.0	0	0.0

Duration of Larval Stadium. To determine the length of the larval period at room temperatures, larvae were reared in shell vials containing soil and raspberry rootlets. The soil was moistened daily and fresh rootlets were added as needed. Under these conditions the minimum time from hatching to pupation was 42 days, the maximum 59 days, with a mean of 50.0 (± 0.3011) days. Larvae were reared on potted strawberry plants in a lath house during June and July. The soil was examined at weekly intervals. The first pupae were found after 42 days, which is also the minimum length of the larval period at room temperature.

Fig. 6.—Larva of the strawberry rootworm. (Ten times natural size.)

Length of Larval Stadium at Various Constant Temperatures. In this test, the larvae were reared in small, covered stender dishes containing a mixture of plaster of Paris, soil, and charcoal (Michelbacher, 1938). A shallow groove, ⅛ inch wide, was prepared in the surface of the plaster. This held the rootlet in place and provided leverage for the larvae. The dishes were watered daily, accumulated frass was removed, and new rootlets were added when

TABLE 11

LENGTH OF THE LARVAL PERIOD OF THE STRAWBERRY ROOTWORM AT VARIOUS CONSTANT TEMPERATURES

Temperature	Period	First instar, days	Second instar, days	Third instar, days	Fourth instar, days	Total days
70° F	Minimum	8	6	9	20	43
	Maximum	21	13	17	30	81
	Mean	13.0	9.3	11.8	23.7	57.8
	P. E.	±0.810	±0.995	±0.595	±2.115	
80° F	Minimum	5	4	4	11	24
	Maximum	14	13	14	20	61
	Mean	7.7	6.5	6.7	13.6	34.5
	P. E.	±0.430	±0.448	±0.570	±0.603	
85° F	Minimum	6	3	4	4	17
	Maximum	9	10	9	17	45
	Mean	6.6	4.8	6.1	10.9	28.4
	P. E.	±0.046	±0.314	±0.304	±0.773	

necessary. One larva only was placed in each dish and each was examined daily under a binocular microscope for moulted skins. The dishes were held at 60°, 70°, 80°, 85°, and 90° F. The larvae could not be reared at temperatures of 60° and 90°F. One larva at 60° moulted for the first time after 20 days, then died. The length of the larval period at the other temperatures is given in table 11, and represented graphically in figure 7.

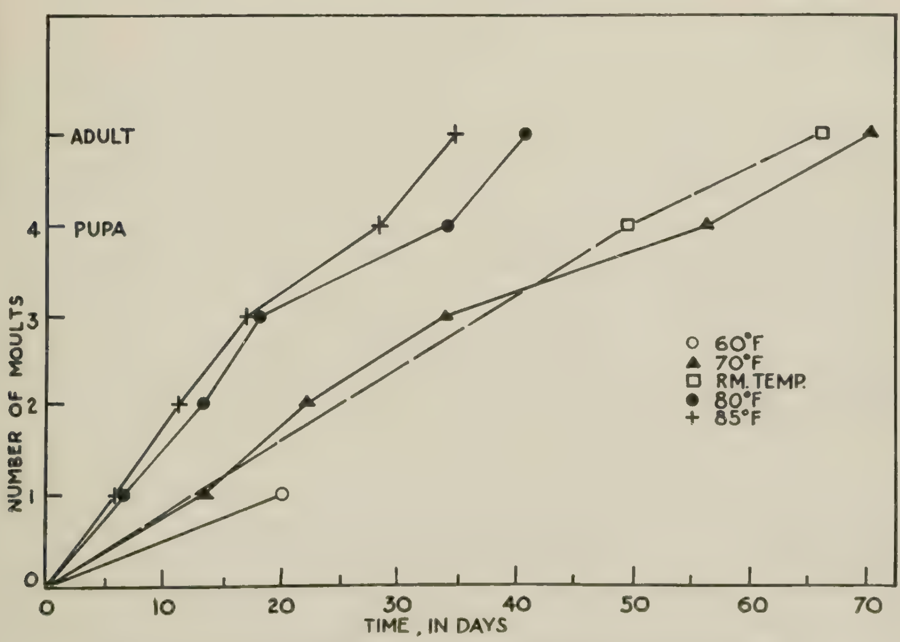

Fig. 7.—Larval and pupal periods of the strawberry rootworm when reared at various temperatures.

PUPAL STADIUM

Prepupal Stage. The prepupal stage starts with the termination of feeding activity by the fourth instar larvae. Ingested food, which appears as a dark reddish brown stripe along the dorsum of feeding larvae, is voided at the beginning of the prepupal stage so that the larvae are white. The body assumes a **C** shape. The only activity of the prepupal larva consists of a twisting motion which is practiced to smooth the inner wall of the pupal cell. The duration of the prepupal stage was measured at two constant temperatures. At 70°F this period averaged 6.60 days, and at 80° it averaged 4.20 days.

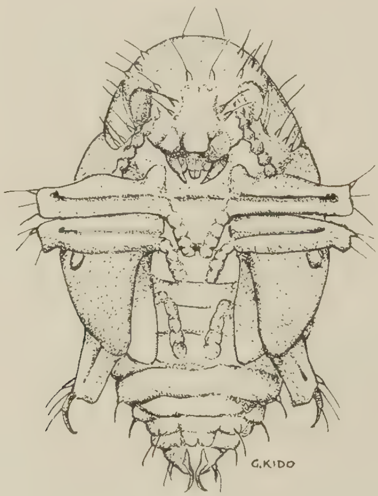

Fig. 8.—Pupa of the strawberry rootworm. (Fifteen times natural size.)

Pupal Stage. Pupae (fig. 8) are located in smooth-walled cells in the soil, distributed as are the larvae (table 10). A series of pupae reared in isolation cages in the laboratory at room temperatures completed the pupal period with a mean of 10.53 days. When reared at constant temperatures of 70°, 80°, and 85°F, means of 12.23 days, 6.75 days, and 5.88 days, respectively, were required for the completion of this stage.

Summary of Developmental Stadia. The total time required to complete the developmental stadia—egg, larva, and pupa—for the temperatures 70°, 80°, and 85°F can be computed by a summation of the means. This is presented in table 12.

SUMMARY

The strawberry rootworm, *Paria canella,* which is recorded from the United States and Canada, is believed to be indigenous to North America. It is present in 28 states and in the District of Columbia. In California, where it is a pest of brambles and strawberries, it is recorded in Alameda, Contra Costa, Merced, Monterey, Placer, Sacramento, San Benito, San Francisco, San Joaquin, San Mateo, Santa Clara, and Yuba counties.

The adults hibernate and emerge in mid-February. The first eggs are deposited toward the end of March or the beginning of April. The first larvae are found around April 15, and the first pupae about June 15. The peak of emergence of new adult forms takes place from July 15 to August 15.

No male forms were found during the investigation, and the females reproduce parthenogenetically.

Paria canella is univoltine, but the longevity of the beetle may extend over one year.

The minimum period of time between the emergence of new adults and the production of eggs, under field temperatures, is 274 days. The ovipositional period extends from April 1— ± 5 days—to the end of September. The average postovipositional period is 29.8 days and terminates about November 15.

TABLE 12

SUMMATION, IN DAYS, OF MEAN PERIODS OF DEVELOPMENT AT CONSTANT TEMPERATURES

Stadium	70° F	80° F	85° F
Egg	12.0	7.2	6.3
Larva	57.8	34.5	28.4
Pupa	12.3	6.8	5.9
Total	82.1	48.5	40.6

Spring emergence may be recorded from the frass production of beetles collected from the field at various time intervals.

Eggs are usually found between two smooth-surfaced objects close to the source of food. The incubation period at room temperatures is 15.95 days. Incubation period at various constant temperatures is given. A single beetle may deposit 207 eggs in its lifetime, although 125 are an approximate average.

The majority of the larvae is found within the first 3 inches under the surface of the soil. At room temperatures, approximately 50 days are required for the larva to reach maturity. At constant temperatures of 70°, 80°, 85°F a mean of 57.77 days, 34.38 days, and 28.31 days, respectively, is required for the completion of the larval period. There are four instars for the larval stage.

The prepupal stages for constant temperatures of 70° and 80°F are 6.66 days and 4.20 days, respectively.

The pupae, like the larvae, are found close to the plant. At constant temperatures of 70°, 80°, and 85°F, a mean of 12.33 days, 6.75 days, and 5.88 days, respectively, is required for the pupal stadium. At room temperatures, the pupal stage required a mean of 10.53 days.

A method of computing the relative amounts of food consumed during the adult stage is given. At room temperatures an average of 1.916 milligrams of food per egg is required from the time the beetles emerge from hibernation to the laying of their first eggs.

Large numbers of beetles were collected and kept at constant temperatures of 45°, 60°, 70°, 80°, and 90°F and a constant humidity of 73 per cent, in order to find the relation between oviposition and temperature. Higher temperatures led to early development of the ovaries and production of more eggs.

LITERATURE CITED

MICHELBACHER, A. E.
1938. The biology of the garden centipede, *Scutigerella immaculata*. Hilgardia **11** (3):55–148.

READIO, P. A.
1939. The strawberry rootworm as a nut pest. North. Nut Growers' Assoc. Proc. **30**: 78, 79.

WEIGEL, C. A.
1926. The strawberry rootworm, a new pest on greenhouse roses. U. S. Dept. Agr. Bul. 1357:1–48.

THE RASPBERRY LEAF SAWFLY

LESLIE M. SMITH AND GEORGE S. KIDO

THE RASPBERRY LEAF SAWFLY[1]

LESLIE M. SMITH[2] AND GEORGE S. KIDO[3]

THE RASPBERRY LEAF SAWFLY (*Priophorus rubivorus* Rohwer)[4] has been present in California for a number of years. In the spring of 1928, the writers found it abundant and widely distributed in the central district of California. It undoubtedly was present there before 1928. Since bush-berry production in the central district was negligible until about 1916, this species could not have been a pest prior to that time.

In midwinter, when the planting stock of bush berries is transported as bare root plants, the sawfly occurs as prepupal larvae and pupae in cocoons in the soil. The chances that the insect will be brought into the state on planting stock consequently are slight. It seems more likely to be native to the Pacific Coast, probably living on wild bush berries prior to the extensive cultivation of horticultural varieties.

Published records indicate that distribution of the pest is limited to California, Oregon, and Washington. In Oregon, the species was described by S. A. Rohwer (1922) from a single female specimen collected on raspberry by E. J. Newcomer at Portland on August 10, 1917. In Washington,[5] in 1937, two specimens were collected on Youngberry at Puyallup; and in 1938, damage to bush berries by this species was reported in the state (Hanson, 1938).

LIFE HISTORY

The eggs of the raspberry leaf sawfly are oval, shining, and opaque white. They measure 0.45 millimeter in width and 1.23 millimeters in length. The female is provided with a saw-type ovipositor which she uses to prepare a cavity in the petioles of leaves or in the tender bark of the new shoots. There she lays her eggs singly between the pith and the bark, placing them parallel to the surface of the bark with the long diameter parallel to the axis of the petiole. At San Jose, the incubation period of the egg ranged from 7 to 9 days under outdoor conditions in June.

The newly hatched larvae feed on the undersides of the leaves, cutting small, roughly circular holes between the veinlets. As they become larger the larvae (fig. 1) eat all the leaf tissue between the main veins. This produces large holes, which, by reason of the arrangement of the leaf veins, are frequently triangular (fig. 2). The larvae are solitary feeders and are always found on the lower side of the leaf. They prefer shade, and are always found in the center and low down in the hedgerow, more commonly on the shady side than on the sunny side. The length of the larval period was not determined experimentally, but field evidence indicates that it is from 4 to 6 weeks.

[1] Received for publication May 12, 1948.

[2] Associate Professor of Entomology and Associate Entomologist in the Experiment Station.

[3] Entomologist, Wisconsin Alumni Research Foundation.

[4] Determined by William Middleton.

[5] Personal communication from C. F. W. Muesebeck.

Fig. 1.—Raspberry leaf showing typical injury and feeding larvae of *Priophorus rubivorus* Rohwer. (Two times natural size.)

Fig. 2.—Raspberry leaves showing injury by the raspberry leaf sawfly.

Mature larvae (fig. 3.) measure 10 to 12 millimeters in length. In diameter the head is smaller than the body, and has three large conspicuous black spots, one on either side and one on the vertex. A broad dark strip extends down the back of the larva. The rest of the body is yellowish white. There is a conspicuous row of tubercles along each side of the body. Although the body is sparsely covered with fine spines it appears nearly "hairless" to the unaided eye.

When the larvae are fully grown they crawl to the ground where they may travel a distance of 10 to 20 feet in search of a suitable place in which to pupate. Pupation usually occurs in wormholes in the highest, driest clods,

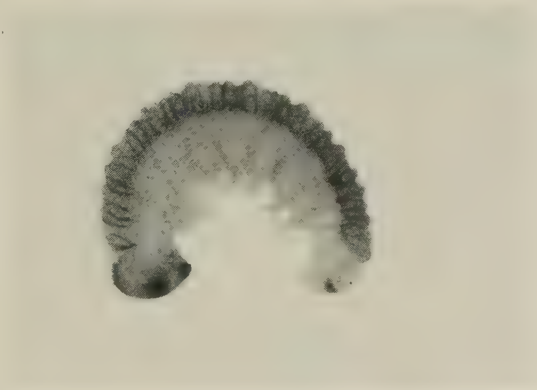

Fig. 3.—Larva of the raspberry leaf sawfly showing characteristic markings. (Five times natural size.)

although artificial sites, such as newspapers and stacked lumber (fig. 4) also offer suitable places.

The larvae spin cocoons in which to pupate. The cocoon consists of a sparsely woven outer structure apparently designed to support and protect the dense inner cylinder in which the larva lies. This inner cylinder is composed of a few threads over which is spread a continuous translucent film. When first constructed, the cocoons are pale yellow, but soon turn pale brown. They become darker with age, so that by spring, overwintered cocoons are chocolate colored. Cocoons of summer generations are empty before darkening can occur.

The length of the pupal period in midsummer was determined by placing mature larvae in battery jars in the laboratory. As soon as they commenced to spin a cocoon they were transferred to other jars and kept at room temperature. Under these conditions the length of time spent in the cocoon varied from 5 to 8 days. This is not the length of the true pupal period, however, since some time may be consumed by the larva in spinning the cocoon and resting before moulting to the pupa.

The adults (fig. 5) are shining black wasplike insects whose antennae, head, and body are shining black, and whose wings are transparent with brownish-black veins. The legs are mostly yellowish white. The antennae vary from 3.0 to 4.0 millimeters in length and the body varies from 5.0 to 6.0 millimeters in

length. They fly readily on warm, sunny, still days. While they do not seem to be capable of making long-sustained, strong flights, they are probably able by means of several successive flights, to travel several miles.

At present this sawfly occurs in practically every raspberry patch throughout the central district of California. Such wide distribution has probably been achieved by flights of the adults. Natural distribution is also enhanced by the fact that all individuals in this species are females; or if males occur they are very rare. Fifty specimens collected at various places at various times were all females. Adults isolated in the pupal stage, which had no contact with

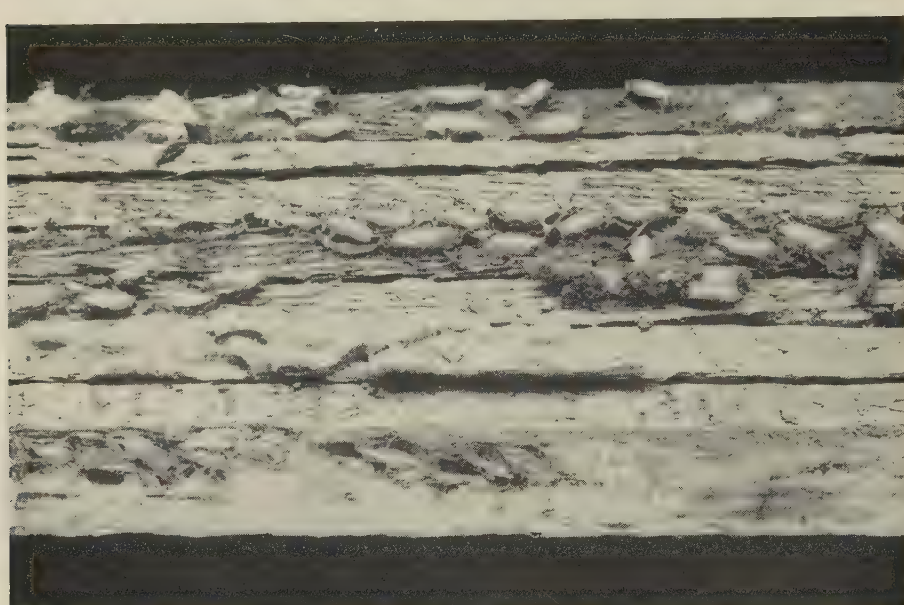

Fig. 4.—Cocoons of the raspberry leaf sawfly adhering to builders' lath stacked adjacent to raspberry bushes.

males, laid eggs which hatched normally. Females lay eggs within 24 hours after emerging from the cocoon. Adult life in the field is probably short. Adults in captivity lived only a few days.

SEASONAL HISTORY

The raspberry leaf sawfly overwinters as prepupal larvae and pupae in cocoons. The adults emerge from the cocoons during April and lay the eggs which give rise to the first brood of larvae. These larvae mature through May and early June. The first adults of the second brood appear about the middle of June. The second brood of larvae reaches a peak about the latter part of July and are nearly all pupated by the early part of August. A partial third brood of adults occurs about the middle of August, and the third brood of larvae occurs throughout September. Some of the larvae of each generation hibernate and emerge as adults the following spring. Hence, there may be

three generations a year. A few feeding larvae found late in October, 1940, are believed to be the offspring of adults whose emergence from the pupae was delayed.

Those larvae which happen to pupate in cool places, such as deep shade or moist soil, probably do not emerge until the following spring, regardless of their generation or time of year. Pupae which were stored in a cool, shaded screened insectary, gave rise to adults after one month. If the temperature

Fig. 5.—Adult female of the raspberry leaf sawfly, *Priophorus rubivorus* Rohwer. (Twelve times natural size.)

had been slightly lower, these pupae would probably have carried through the winter. In Washington (Hanson, 1938) there is generally a single generation a year, but a few adults emerge and give rise to a partial second generation each year.

The larvae reach a peak of abundance and destructiveness in June, and decrease in abundance throughout the summer and fall. This means that the first or spring brood of larvae are the most destructive. This is probably due to the fact that a large proportion of each generation remains in the cocoon until the following spring, at which time they all emerge. The prolongation of the pupal period is probably the result of lower temperatures. To some extent the decrease in abundance of sawflies throughout the summer and fall may be due to parasitism. Either parasitic or climatic checks on this pest may occa-

sionally be lifted, possibly causing an outbreak in the fall; but in the past twenty years, during which time the writers have had the pest under observation, the peak of abundance and injury has occurred in June.

The raspberry leaf sawfly varies greatly in abundance over a period of years. In occasional years in the central district it is so scarce that it is not a pest in any raspberry patch; but in other years it is abundant in all patches and seriously destructive in some. During the last twenty years it has reached three peaks of abundance: in 1928, 1933, and 1940. These outbreaks and recessions are believed to be caused by a fluctuating balance with the two species of parasite which are discussed in the section on parasites.

HOST PLANTS

In the central district the raspberry leaf sawfly is most commonly found on the Ranere (St. Regis) raspberry—the most extensively grown raspberry. In a few instances in the field the relative susceptibility of various brambles to attack was estimated. On one ranch, Ranere raspberries, Red Loganberries, and Himalaya blackberries were growing in contiguous patches. The Ranere raspberries were seriously defoliated, and the Loganberries were slightly damaged. The blackberries were not damaged to any appreciable extent, although some larvae were feeding on them. It seems likely that this sawfly can complete its life cycle on blackberry but does not do so by choice. On another ranch, Ranere raspberries, Cuthbert raspberries, and Youngberries were growing in contiguous patches. The Ranere and Cuthbert raspberries were severely and equally damaged. The Youngberries were damaged, but much less so than the raspberries.

From these observations it seems that raspberry is the preferred host, and that various varieties may be equally attacked. Loganberries and Youngberries are less susceptible but may suffer commercial damage, while blackberries are seldom, if ever, injured sufficiently to warrant control measures.

PARASITES

The raspberry leaf sawfly is heavily parasitized at times by two internal parasites: (1) a small fly, *Bessa selecta* (Meigen), and (2) a minute wasplike insect, *Dibrachys boucheanus* (Ratz).[6] Pupae of the sawfly were found to be heavily parasitized by *B. selecta* in the fall of 1933, following a serious outbreak of the sawfly that year. This parasite pupates within the skin of the sawfly inside the cocoon, and emerges as a small gray fly the following spring. It is world wide in distribution and attacks many species of sawflies.

The wasplike parasite, *D. boucheanus* (Ratz), is black, and the females measure about 2 millimeters in length. Both males and females occur, and the males are only about half as large as the females. After mating, the females oviposit in prepupal sawfly larvae within their cocoons. In the laboratory a generation of the parasite was completed in 12 days at room temperature. The parasites pupate inside the sawfly cocoon, but outside the larval skin of the sawfly. Usually from 20 to 25 parasites mature in each sawfly cocoon. The

[6] Determined by A. B. Gahan.

parasites pass the winter as mature larvae within the sawfly cocoon. Pupation occurs in the spring, and the adult parasites emerge a few days later.

This parasite is world wide in distribution, and has been recorded as acting as a hyperparasite upon a number of other parasites. Whether or not it would act as a hyperparasite on *B. selecta* is not known, but laboratory rearings on sawfly larvae definitely known not to be infested with *B. selecta* have established the fact that *D. boucheanus* can act as a primary parasite on the sawfly larvae. Field evidence indicates that *D. boucheanus* is seldom, if ever, hyperparasitic on *B. selecta.*

CONTROL

The larvae of the raspberry leaf sawfly can be killed with a thorough application of a one half per cent rotenone dust. This will require from 50 to 75 pounds of dust per acre, depending on the size of the bushes. If no suitable power dusters are available the dust should be applied with a rotary knapsack type of duster. Dusters of the bellows type do not produce an even coverage on raspberries grown in a hedgerow system. The dust should be directed upward from below, in an attempt to blow dust on the undersides of the leaves, since the larvae are always found on the lower leaf surface. The dust should be blown particularly into the interior of the hedgerow since this is the favorite locality for the larvae.

Dusting should be done whenever damage by the larvae reaches economic proportions. However, growers should remember that the sawfly usually decreases in abundance after June, and dustings after this date will usually not be necessary.

OTHER SAWFLIES ON RASPBERRIES

The raspberry leaf sawfly should not be confused with two other species of sawflies occurring on raspberry foliage. These are: (1) the eastern raspberry sawfly, *Blennocampa* (*Monophadnoides*)[7] *rubi* (Harris), and (2) the red sawfly, *Tenthredo xanthus* Nort.[4]

Raspberry Sawfly. The name "raspberry sawfly" has been approved by the American Association of Economic Entomologists to represent *B. rubi;* hence, the name "raspberry leaf sawfly" is used herein to designate *Priophorus rubivorus* Rohwer.

The larvae of these two sawflies are easily distinguished, since *B. rubi* is pale green with white tufts of spines arising from body tubercles, arranged in rings around the body. This causes the larvae to appear quite "hairy" to the unaided eye. The larvae of *P. rubivorus,* on the other hand, appear almost "hairless" to the unaided eye. The adults of these two species are quite similar in appearance and can be positively identified only by a taxonomist.

The damage done by the larvae in feeding on the foliage of raspberries is likewise distinct in these two species. The raspberry sawfly (*B. rubi*) prefers to feed in the tops of the bushes on the young tender leaves, whereas the raspberry leaf sawfly (*P. rubivorus*) feeds on the old leaves in the deepest shade

[7] The generic name *Monophadnoides* has been suppressed as a synonym of *Blennocampa.* (In a personal communication from E. A. Chapin.)

in the center of the hedgerow. When the larva of the raspberry sawfly is disturbed (Flint, 1940), it raises its head and tail end of the body, whereas the larva of the raspberry leaf sawfly, when disturbed, curls its body into a spiral.

Distribution of Raspberry Sawfly. During the past few years, the raspberry sawfly (*B. rubi*) has been reported injuring raspberries in Connecticut, Idaho, Illinois, Kansas, Michigan, Montana, New York, Ohio, and Oregon.[8] All of these states, with the exception of Kansas, are north of 40° latitude. This might be taken as evidence that this sawfly is limited to northern states

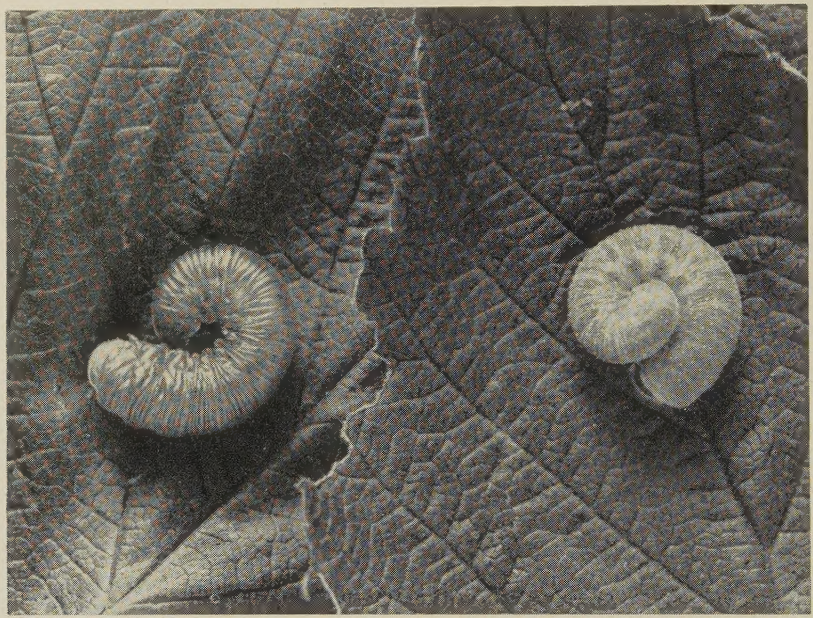

Fig. 6.—Larvae of *Tenthredo xanthus* Nort,[4] showing typical resting position. Left, mature feeding larva; right, mature larva which has stopped feeding and is ready to pupate. Note ragged leaf edge caused by these larvae. (Two times natural size.)

in its geographic distribution. However, in 1930, the first 11 leading states in raspberry acreage were all north of 40° latitude. Not once during the past twenty years when the writers have had frequent occasion to visit raspberry patches in the central district of California have specimens of the raspberry sawfly been found. It seems probable that this pest is not present in California.

Red Sawfly. Another species of sawfly occasionally occurs on raspberries in California. This species, which is herein called the red sawfly, *Tenthredo xanthus* Nort.,[4] is of slight economic importance. During the past twenty years no infestation of this insect, which warranted control measures, has come to the attention of the authors. The adults are easily distinguished by their brilliant red and black coloring and their large size. The female is approximately one half inch long, with red body, legs, and head. The eyes and ocelli are black; the basal two joints of the antennae are red, and the rest of the antennae is black. The wings are blue black with a faint yellow spot on

[8] From notes by various reporters in the Insect Pest Survey Bulletin, 1934–1939.

the front margin. The labrum and palpi are yellow. The thorax is black below, and a few irregular black blotches occur on the venter of the abdomen.

The larvae (fig. 6) are large pale green worms with minute white flecks on their bodies. They are almost devoid of hair. During the day they lie curled in a spiral on the upper surface of a leaf which is overlapped by another leaf.

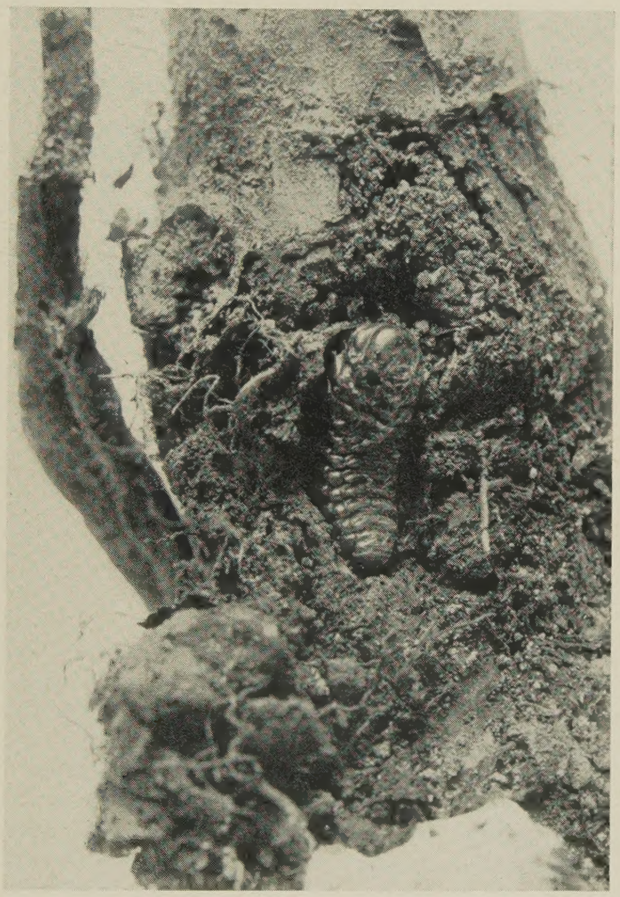

Fig. 7.—Raspberry crown showing prepupal and pupal chamber of *Tenthredo xanthus* Nort.[4] (Two times natural size.)

Because of this habit and because of their coloration, they are very difficult to see. These larvae, unlike those of *B. rubi* and *P. rubivorus,* feed entirely on the edge of the leaf where they produce large irregular gaps in the leaf margin. When mature, the larvae drop to the ground and burrow into dead and rotted raspberry crowns, where pupation occurs (fig. 7).

Adults emerged in screen cages out of doors during the latter part of March, and were seen in the field until the end of April. By the middle of June, larvae in the field ranged from about half grown to fully grown. The winter is passed in the pupal or prepupal stage within the pupal cell.

LITERATURE CITED

FLINT, W. P.
1940. Bramble fruits, Part III. Bramble insects and their control. Illinois Agr. Exp. Sta. Cir. **508**:1–71.

HANSON, A. J., AND R. L. WEBSTER.
1938. Insects of the blackberry, raspberry, currant, and gooseberry. Washington Agr. Exp. Sta. Pop. Bul. **155**:1–38.

ROHWER, S. A., AND WILLIAM MIDDLETON.
1922. North American sawflies of the subfamily Cladiinae. U. S. Natl. Mus. Proc. **60**(1):1–46.

4*m*-3,'49 (B1649)

141